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A male spider's ornamentation polymorphism maintained by opposing selection with two niches

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Abstract
The Levene mechanism to maintain genotypic polymorphism by opposing selection on genotypes in multiple niches was proposed 60 years ago, and yet no systems were found to satisfy the mechanisms rather restrictive conditions. Reported here is such an example that a wolf spider population lives in a habitat of mixed rocks and leafy litter for which the females are phenotypically indistinguishable and the males have two distinct phenotypes subject to opposing selection with respect to the substrates. Census data is best-fitted to a population genetics model of the Levene type. A majority of the best fit support polymorphism, with many fitted parameter values quantitatively consistent with various laboratory studies on two closely related species.

Keywords: Female choice, population genetics model, S*chizocosa, S. ocreata, S. rovneri*

1. Introduction

How nature maintains its immense genetic variation is still one of the open questions in biology. Selection has been thought to play a major role since Fisher (1922) showed that polymorphism is possible if a population's heterozygote is fitter than both of its homozygotes of which systems have been found but shown to be rare (Hedrick, 2012). Levene (1953) proposed a polymorphic mechanism by opposing selection on genotypes with multiple niches, but there was no real system that was shown to be his case despite reasonable scenarios having been suggested (Chunco et al., 2007). One explanation for the lack of examples, suggested by Prout (2000), was that the parameter region for Levene's polymorphism is too restrictive if the opposing fitnesses have a small separation which was thought to be expected (Maynard Smith, 1966; Maynard Smith, 1970). The aim of this paper is to present a plausible system for Levene's case.

The system under consideration is a syntopic population of wolf spiders from the genus *Schizocosa* that exhibits the male ornamentation polymorphism (MOP). In Stratton and Uetz, 1981; Stratton and Uetz, 1983, *S. ocreata* and *S. rovneri* were characterized as an ethospecies, reproductively isolated only by female discrimination of species-specific male courtship. *S. ocreata* possess decorative tufts on their forelegs which they use during courtship as visual and seismic cues (Roberts et al., 2006; Gibson and Uetz, 2008; Uetz et al., 2009), whereas *S. rovneri* possess no such decoration. Although mature males of the two species are noticeably different phenotypically, the genitalia and the morphology of the females from their respective populations cannot be distinguished. Artificial cross breeding in captivity (Stratton and Uetz, 1986, Table 4) suggests that this male dimorphism is autosomal. This limited study shows that it is approximately Mendelian but without a clear determination on whether the non-ornamentation trait is recessive or dominant. It is not known how the dimorphic trait is suppressed in the females. Some genetic switch mechanisms that are responsible for a dimorphic trait of *Drosophila* (Williams and Carroll, 2009) may play a similar role.

Typically these two species are geographically isolated, but in 2004 Hebets and Vink (2007) located a population of *Schizocosa* in which males similar to both species were found co-occurring, Table 1. Microsatellite analyses of males from this mixed-phenotype population as well as from pure *S. ocreata* and *S. rovneri* populations establish that males from the mixed population are genetically indistinguishable from each other, yet are genetically distinct from their closest relatives *S. ocreata* and *S. rovneri* (Fowler-Finn, 2009). These dimorphic males live syntopically in a habitat of mixed substrates. The population spans distinct substrate-types of rocks and leafy litter, suggesting that spatial heterogeneity may play an important role for this dimorphic coexistence. Through experimentation, the authors also demonstrated that imprinting of females may be important in mate choice decisions and as such, may be involved in the maintenance of this polymorphism.

Mate choice learning in the form of imprinting is well documented in spiders (Hebets, 2003; Hebets and Vink, 2007). Specifically, oblique imprinting by which individuals develop their mate preferences by imprinting on their coetaneous peers is known to occur in *Schizocosa* (Kirkpatrick, 1982; Liou and Price, 1994; Verzijden et al., 2005; Tramm and Servedio, 2008). In the field, males mature on average a few weeks prior to females (Hebets, 2003), which is the likely developmental period for imprinting to occur. Observations show that females from this mixed-phenotype population who experience courtship displays of mature males during subadulthood mate significantly (3.0–6.5 times) more with brush-legged males, regardless of the phenotype of their exposure male, whereas inexperienced females do not demonstrate such mate preference (Hebets and Vink, 2007). In addition, population density in this mixed population can be considerable with more than 3 individuals per 100 cm^2 (Fowler-Finn and Hebets, 2011b), making it reasonable to assume that all penultimate females would have encountered mature males before maturation. As females tend to mate only once (Norton and Uetz, 2005), the females' prior experience may be integral in determining the frequencies of the two male phenotypes in the population.

Differential mating success for brush-legged and non-ornamented males has also been linked to environmental conditions. The mixed population site is unique in this regard. Previous studies (Stratton and Uetz, 1981; Stratton and Uetz, 1983) have revealed the important role that substratum characteristics play in courtship efficacy between *S. ocreata* and *S. rovneri*. In Scheffer et al. (1996), the authors demonstrated that vibratory communication is constrained by the leaf litter habitat. Hence the leafy substratum may create an important physical constraint for ornamented males, hindering the effectiveness of their visual and vibrational signalling. Experimental data suggests that brush-legged males receive a mating advantage on rocky terrain, but no significant advantage in the leaf litter substratum, presumably due to the vibrational interference (E. Hebets, unpublished data).

While the ornamentation may enhance the fitness of the brush-legged male form through its increased mate acquisition, it may simultaneously decrease it by attracting the attention of predators (Burk, 1982; Magnhagen, 1991; Pruden and Uetz, 2004; Roberts et al., 2006; Fowler-Finn and Hebets, 2011a). Due to the increased visibility of their foreleg ornamentation, brush-legged male wolf spiders are more susceptible to predators than non-ornamented males. The large wolf spider *Hogna helluo*, common to deciduous forests, preys upon both *S. ocreata* and *S. rovneri*, but exerting greater pressure on the former because it uses visual cues (Pruden and Uetz, 2004). Similarly, when preying upon males from the mixed-phenotype population, *Hognai* attacked brush-legged males sooner (two times) than non-ornamented males, though overall predation rates did not differ between the male forms (Fowler-Finn and Hebets, 2011b). Avian predators may differentially prey on the two forms as well (Pruden and Uetz, 2004; Roberts et al., 2006; Roberts and Uetz, 2008) as the rock background makes the brush-legged males more conspicuous.

Obviously the mixed-site's MOP cannot be explained by the theory of opposing selection on sexes (Haldane, 1962; Kidwell et al., 1977) because the sexual selection by the female spider on the dimorphic males is unidirectional. It cannot be explained by differential natural selection alone since the female spiders mate preference can potentially negate the effect of predation on the brush-legged males. The habitat heterogeneity also plays a direct role in creating the various opposing selectivities on the male phenotypes. All these factors make the mixed-population an ideal candidate for Levene's polymorphism theory. The quantitative question to ask is is the mixed population a case of his theory and to what extent is a fit a good fit?

2. Two-niche dioecious population model

Strictly speaking, Levene's model does not apply to the mixed-population because it does not include differential selection on the two sexes which is the case for the spider system. Without differential selection on sexes, Levene's model is one-dimensional. With it, such a model is two-dimensional (Haldane, 1962; Kidwell et al., 1977; Ewens, 1979; Hartl and Clark, 1988). Except for this distinction, the model under consideration for the spider system is similar to Levene's. The following assumptions are made:

- The spider population is large and the generations are non-overlapping.
- Individual spiders move around proportional to the substrate ratio without preferential niche selection, i.e. the population is selected by the habitat.
- All female spiders are imprinted before maturation and prefer to mate with brush-legged males.
- Female spiders are monomorphic, and both natural and sexual selections act disproportionately on the male phenotypes which are autosomal.
- All disproportionate selective parameters on the male forms are density independent.

The deterministic model is to track the genotypic frequencies of zygotes from one generation to the next because of the tacit assumption that the population is approximately infinity.

Let a and A denote the non-ornamented allele and the brush-legged allele, respectively. Let p be the allele frequency of a and q be the allele frequency of A at birth. We will use notation $pa : qA$

Table 1. Mixed population data in percentage (and sample size).

Male form		2004	2005		2006		2007	2008	
	Rocks	Rocks	Litter	Rocks	Litter	Rocks	Litter	Rocks	Litter
Non-ornamented	40	22 (19)	56 (48)	21 (12)	63 (108)	15 (2)	63 (42)	20 (1)	64 (63)
Brush-Legged	60	78 (66)	44 (38)	79 (45)	37 (64)	85 (11)	37 (25)	80 (4)	36 (36)

Percentage of rocks: 5–15%

to denote this correspondence and similar notations for other ratio vs. type correspondences. Let *aa, aA, AA* denote the genotypes and $xaa : yaA : zAA$ be the corresponding genotypic frequencies at birth. Then $p = x + \frac{1}{2}y$, $q = 1 - p = z + \frac{1}{2}y$. The genotypic distribution is the same for both sexes at birth. Let $x'aa : y'aA : z'AA$ and $p'a : q'A$ be the same type frequencies for the offspring generation at birth. Since it is not known at this point which allele type is dominant, we will consider two cases: *a* being recessive and dominant. Both cases are mathematically similar. We only need to present one case in detail and adapt it to the other accordingly.

Consider first the *a*-recessive case. Let $1aa : u_i[aA+AA]$ be the natural selection parameter ratio for the male genotypes with $i = r$ for the rocky substrate and $i = \ell$ for the leafy substrate. Let $1aa : v_i[aA+AA]$ be the corresponding sexual selection parameter ratio. Then the overall substrate-specific selection parameter ratio or the fitness ratio becomes $1aa : w_i[aA + AA]$ with $w_i = u_i v_i$ for $i = r, \ell$ (Appendix A). Hence, the male spider's genotypic distributions conditioned on the individual substrates at reproduction are

$$x_{m,i} = \frac{x}{x + w_i(1-x)}, \quad y_{m,i} = \frac{w_i y}{x + w_i(1-x)}, \quad z_{m,i} = 1 - x_{m,i} - y_{m,i}.$$

Since the female spiders are not differentially affected by either selection or spatial heterogeneity, their genotypic probability distribution remains unchanged from birth to maturation in both substrates, i.e. $x_{f,i}aa : y_{f,i}aA : z_{f,i}AA = xaa : yaA : zAA$. Thus, given that mating takes place in substrate *i*, the conditional zygotic distribution becomes

$$\begin{cases} x_i' = p_{m,i}p_{f,i} = \left(x_{m,i} + \frac{1}{2}y_{m,i}\right)\left(x + \frac{1}{2}y\right) \\ y_i' = p_{m,i}q_{f,i} + q_{m,i}p_{f,i} = \left(x_{m,i} + \frac{1}{2}y_{m,i}\right)\left[1 - \left(x + \frac{1}{2}y\right)\right] + \left[1 - \left(x_{m,i} + \frac{1}{2}y_{m,i}\right)\right]\left(x + \frac{1}{2}y\right) \end{cases} \quad (1)$$

where $p_{j,i}, q_{j,i}$ denote the allelic probabilities for sex *j* in substrate *i*. Since the habitat is distributed by the substrate ratio *r* rock : $(1 - r)$ litter, the new generation's genotypic probability distribution at birth becomes

$$x' = x_r' r + x_\ell'(1-r), \qquad y' = y_r' r + y_\ell'(1-r) \quad (2)$$

with $z' = 1 - x' - y'$ omitted. This completes the probabilistic model in recursive relation.

To find polymorphic equilibrium points, we transform the genotypic relationships (2) in terms of *x* and $p = x + \frac{1}{2}y$ instead to get (Appendix B)

$$\begin{cases} x' = p^2 + p(1-p)x\phi(x, w_r, w_\ell, r) \\ p' = p + \frac{1}{2}(1-p)x\phi(x, w_r, w_\ell, r) \\ \text{with } \phi(x, w_r, w_\ell, r) = \frac{1 - w_r}{w_r + (1-w_r)x} r + \frac{1 - w_\ell}{w_\ell + (1-w_\ell)x}(1-r) \end{cases} \quad (3)$$

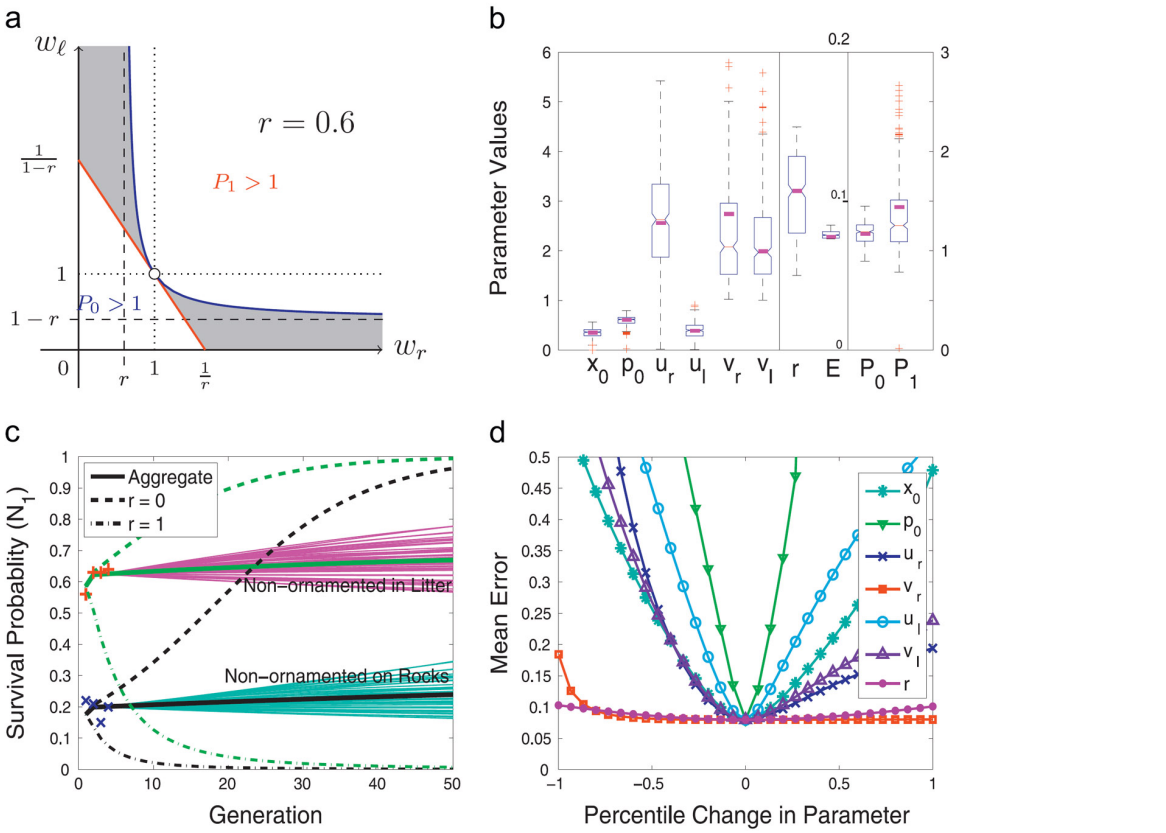

Figure 1. (**a**) In the $P_1 > 1$ and unshaded region the fixation point $(x, p) = (0, 0)$ is globally stable because $P_0 < 1$. In the $P_0 > 1$ and unshaded region the fixation point $(x, p) = (1, 1)$ is globally stable because $P_1 < 1$. The shaded region is the region of polymorphism where both $P_0 > 1$ and $P_1 > 1$ hold. The parameter point (1, 1) is the Hardy–Weinberg point at which the niche fitnesses are all neutral $w_r = w_\ell = 1$. Notice that as *r* changes from 0 to 1, the polymorphism region sweeps the regions of $w_r > 1$, $w_\ell < 1$ and $w_r > 1$, $w_\ell < 1$, which are necessary but not sufficient conditions for polymorphism. (**b**)–(**d**) are for the *a*-recessive case. (**b**) Boxplot for the 365 best fits in the range $0.05 < r < 0.15$ and $v_r, v_\ell \geq 1$. The thick bars mark the best-fit that is nearest the mean of the parameters of the 365 best fits. The scale for parameter *r* and the error *E* are given along the second inserted line from the left. The scale for P_0, P_1 is given along the right side of the box. (**c**) The +, × markers are the data points. The aggregated fit is the average of the model runs, individually at each generation and over the best 50 fits which are the thin lines. The aggregated fit from more best fits or all the best fits deviates little except that individual fits spread out more than the subset shown. The dashed population runs are for the best model fit parameters except for the *r* values. (**d**) The averaged sensitivity plot over all 365 best fits individually at each discretized percentile change. It shows that a typical best fit is least sensitive to parameters *r* and v_r.

This form allows us to find conditions for protected polymorphism (Levene, 1953; Prout, 1968) easily. To show the trivial fixation equilibrium point $x = p = 0$ is unstable, we only need to show $\Delta p = p' - p > 0$ for sufficiently small x, p, equivalently, $2\Delta p/(1-p)x|_{x=p=0} = \phi(0, w_r, w_\ell, r) > 0$, which is simplified as

$$P_0(w_r, w_\ell, r) := \frac{1}{w_r} r + \frac{1}{w_\ell}(1-r) > 1 \tag{4}$$

Similarly, to show the other trivial fixation equilibrium point $x = p = 1$ is unstable, we need $\Delta p = p' - p < 0$ for point near $x = p = 1$, which is equivalent to $2\Delta p/(1-p)x|_{x=p=1} = \phi(1, w_r, w_\ell, r) < 0$, or

$$P_1(w_r, w_\ell, r) := w_r r + w_\ell(1-r) > 1 \tag{5}$$

When these two conditions are met, there is a polymorphic equilibrium point $0 < \bar{x} < 1$ with $\phi(\bar{x}, w_r, w_\ell, r) = 0$ and $\bar{p} = \sqrt{\bar{x}}$. In fact, these two conditions are also necessary since the polymorphic equilibrium point can uniquely be solved as

$$\bar{x} = -\left[\frac{w_\ell}{1-w_\ell} r + \frac{w_r}{1-w_r}(1-r)\right] \tag{6}$$

for which it is easy to show $0 < x < 1$ if and only if $P_0 > 1$, $P_1 > 1$. In the parameter space (w_r, w_ℓ, r), the polymorphism region is bounded by the bifurcation surfaces at which $\bar{x} = 0$ and $\bar{x} = 1$, which are given by the equalities of (4) and (5), respectively: $P_0 = P_1 = 1$. One can prove that the equilibrium point $\bar{x}$ is stable but a proof is omitted here. Figure 1(a) shows the regions for a fixed r value. Note from (4) and (5) that the net selection must be opposing, $w_r > 1 > w_\ell$ or $w_r < 1 < w_\ell$, in order for the protected polymorphism to exist as the two inequalities fail to hold simultaneously if both $w_r, w_\ell > 1$ or both $w_r, w_\ell < 1$. Also note that the polymorphism equilibrium point is necessarily Hardy–Weinberg type as $\bar{x} = \bar{p}^2$ (Hardy, 1908; Weinberg, 1908).

We now adapt the analysis above to the a-dominant case. Here the definitions of the parameters remain the same because they are phenotypic. Mathematically, we can treat this case symmetrically. In particular, let $u'_i = 1/u_i$, $v'_i = 1/v_i$ and $w'_i = 1/w_i$. Then the assumption $1[aa{+}aA] : u_i AA$ translates to $u'_i[aa{+}aA] : 1AA$, and the same for v_i and w_i, etc. In this case, AA is the recessive genotype, and instead of x, p we use z, q to represent the model, analogous to Equation (3):

$$\begin{cases} z' = q^2 + q(1-q)z\phi(z, w'_r, w'_\ell, r) \\ q' = q + \dfrac{1}{2}(1-q)z\phi(z, w'_r, w'_\ell, r) \\ \text{with } x = 1-y-z = 1-2(q-z)-z \text{ and } p = 1-q \end{cases} \tag{7}$$

and with exactly the same functional ϕ as before. As for the protected polymorphism conditions, we have analogously, $P'_0(w'_r, w'_\ell, r) = r/w'_r + (1-r)/w'_\ell = rw_r + (1-r)w_\ell > 1$ and $P'_1(w'_r, w'_\ell, r) = rw'_r + (1-r)w'_\ell = r/w_r + (1-r)/w_\ell > 1$. Since $z = q = 0$, $1 \Leftrightarrow x = p = 1, 0$, we have $P'_0(w'_r, w'_\ell, r) = P_1(w_r, w_\ell, r)$ and $P'_1(w'_r, w'_\ell, r) = P_0(w_r, w_\ell, r)$, exactly the same protected polymorphism conditions as for the first case, and the same bifurcation diagram as well (Figure 1(a)). As for the polymorphism equilibrium point we have $\bar{z} = -[r/(w_\ell - 1) + (1-r)/(w_r - 1)]$ and $\bar{x} = (1 - \sqrt{\bar{z}})^2$ for being the Hardy–Weinberg type.

We end this section by noting the following. A similar model to (2) was introduced in Chunco et al. (2007) which assumes instead that the male dimorphic gene is on the X-chromosome, resulting in a haploid–diploid hybrid version of our model. Although the Levene type models are one dimensional for non-differentially selected sexes, the conditions for protected polymorphism, $P_0 > 1, P_1 > 1$, for his type and ours turn out to be the same (cf. Prout, 1968; Maynard Smith, 1970). Other polymorphism mechanisms with temporal variation, opposing sexual selection, and sex-linked selection (Haldane, 1962; Haldane and Jayakar, 1963; Haldane and Jayakar, 1964) are less relevant to the spider system and therefore not factored into our model.

3. Best model fit to the mixed wolf spider population

The line search method: Let $d_{r,i}$ denote the observed frequency for the non-ornamented male spiders on rocks from Table 1, with $i = 0$ corresponding to the year 2004 and $i = 1$ the year 2005 and so on. Similarly, $d_{\ell,i}$ denotes the observed frequency for the non-ornamented male spiders in litter. The 2004s data in litter was not collected. (Only those data points for non-ornamented males are used since the data for brush-legged males are complementary.) Since we assume what we observed was the survival probabilities with the natural selection parameter ratio: $1aa : u_i[aA{+}AA]$ for the a-recessive case, the corresponding predicated probabilities are

$$N_1(x, u_i) = \frac{x}{x + ui(1-x)} \quad \text{and} \quad N_2(x, u_i) = \frac{u_i(1-x)}{x + ui(1-x)}$$

for non-ornamented male spiders and brush-legged male spiders, respectively, with $i = r, \ell$. For the a-dominant case, the ratio is $1[aa + aA] : u_i AA$ and the corresponding predicated probabilities are (for a minor abuse of notation)

$$N_1(z, u_i) = \frac{1-z}{1-z+u_i z} \quad \text{and} \quad N_2(z, u_i) = \frac{u_i z}{1-z+u_i z}$$

In each case the N_1 and N_2 are complementary as $N_1 + N_2 = 1$. As a result only one of them is needed for the error function between the observed and the predicted. We will use N_1 for both habitat substrates. Using N_2 gives rise to the same result. Hence, the error function E is defined as follows:

$$E(\rho) = E(\rho^*) + \sum_{i=1}^{7} \frac{1}{2}\frac{\partial^2 E}{\partial \rho_i^2}(\rho^*)(\rho_i - \rho_i^*)^2 + \cdots \tag{8}$$

with $\eta = x$ for the first case and $\eta = z$ for the second case. Here $\rho = (x_0, p_0, u_r, v_r, u_\ell, v_\ell, r)$ denotes the vector of the initial frequencies x_0, p_0 and the model parameters, all of which need to be determined in order to minimize the error $E(\rho)$. Also $\omega_{r,i}, \omega_{\ell,i}$ are the weight parameters for the errors, determining how much of a weight each years data should be accounted toward the total deviation. That is always $\omega_{\ell,0} = 0$ since the litter data was not collected for 2004. For this paper we have considered the best model fit to two different combinations of the data, referred to as *the* 04–08 *data* with all $\omega_* \equiv 1$ except $\omega_{r,4} = 0$, and *the* 05–08 *data* with all $\omega_* \equiv 1$ except $\omega_{r,0} = 0$. That is, we exclude the 2008 data on rocks from the 2004–2008 fit since the sample size is too small, but include it to the 2005–2008 fit since the corresponding percentage is in the same range as the other years. Simulation results are similar for both data combinations. As a result only the 05–08 simulation is presented hereon.

We note that because the error function $E(\rho)$ sums over the length of the data, once found the best fitted initial values and parameters do not change over the length of the data. However, if we limit the error function to 1 year in length, including only the current years and the next years data, we can create a sequence of four or five error functions, $E_i(\rho)$, each of which can be best-fitted 1 year a time to result in a changing sequence $\rho(i)$ in the population frequencies and in the parameter values. Deviations in the changing parameters from their means can be used to measure or to model environmental fluctuations. For example, if the change in the predation parameter in a given year matches that year's change in the field, then it can be considered to have established a causality for that year's fluctuation in the population. Since we do not keep track of such environmental changes in our model, mostly due to the lack of such data, the error function variable ρ consists of the true initial frequencies

and the true parameters for the model. The alternative approach by the changing error function $E_i(\rho)$ in time suggests an effective way to study the impact of a noisy environment on population, which we will not pursue further in this paper.

The essential approach to minimizing $E(\rho)$ is by Newton's gradient search by which we look for a smaller error $E(\rho_{k+1})$ at a new initial and parameter point ρ_{k+1} from a current point ρ_k. The least complicated but a very effective implementation is the line search method (Ruszczynkski, 2006) for which a case of its application to an ecological problem can be found in Deng (2014). The line search method works as follows. We first start the search at a user dependent initial guess, ρ_o, often at random. Then for each component i of ρ we fix all other component values $\rho_{o,j}$, $j \neq i$ and search for a smaller error $E(\rho)$ by varying only the ith component in the double-ranged interval $(0,2\rho_{o,i})$. We will carry out this "line search" at a discrete set of points of the interval, say $2K + 1$ points with a regular increment $\rho_{o,i}/K$ from 0 to $2\rho_{o,i}$. That is, we will compute the error at K many points to both sides of the initial guess $\rho_{o,i}$. We will do this for all components of the initial guess ρ_o with the same discretizing integer K. By the end of this first round search, we would have generated $2K \times 7 + 1$ many points in ρ and the same number of values for the error function $E(\rho)$ with the number 7 being the dimension of ρ and the one center value $E(\rho_o)$ all component line searches share. Of these points we find the next new initial guess ρ_1 at which $E(\rho_1)$ is the smallest. We will continue this iteration until a local minimum ρ^* is reached, i.e. the successive $E(\rho_k)$ are within a preset tolerance δ. The initial and parameter values ρ^* are then considered to be best-fitted of the model to the data. $K = 50$, $\delta = 0.001$ were used for this paper.

Sensitivity to best fit : At a local minimum point ρ^* for the error function $E(\rho)$, the question is how sensitive is the local minimum value $E(\rho^*)$ to changes in the parameters from the point ρ^*? Assume the local minimizer ρ^* is an interior point, then the first partial derivatives of E vanish at the point, and by the Taylor expansion we have

$$E(\rho) = E(\rho^*) + \sum_{i=1}^{7} \frac{1}{2} \frac{\partial^2 E}{\partial \rho_i^2}(\rho^*)(\rho_i - \rho_i^*)^2 + \cdots$$

For an interior point ρ^*, each component $\rho^*_i > 0$, and hence we can rewrite the expansion above as follows:

$$E(\rho) = E(\rho^*) + \sum_{i=1}^{7} \frac{(\rho_i^*)^2}{2} \frac{\partial^2 E}{\partial \rho_i^2}(\rho^*) \frac{(\rho_i - \rho_i^*)^2}{(\rho_i^*)^2} + \cdots$$

making the squared change dimensionless. By definition, the coefficient of the squared percentage change is the *sensitivity* of the error with respect to the ρ_i parameter:

$$S(\rho_i) := \frac{(\rho_i^*)^2}{2} \frac{\partial^2 E}{\partial \rho_i{}^2}(\rho^*) \tag{9}$$

Notice that for a same small percentage change the error E becomes larger in component ρ_i if its sensitivity value $S(\rho_i)$ is larger than the rest.

Model test: The global minimum of E can be found in a probabilistic and asymptotic sense if we repeat the random search indefinitely. In practice we can only run the search for a finite time. Thus the resulting local minimum from a time-limited run is only a provisional global minimum. Also for far too many cases the local minimums are too close to tell them apart (for being within the preset tolerance for the searched error), and thus equal consideration needs to be given for these indistinguishable local minimums. Of which, some predict a brush-legged fixation ($P_o < 1$), while some others predict a non-ornamented fixation ($P_1 < 1$), and so on. If a majority of the best fit is say for polymorphism then we declare that the empirical system is predicted by the model of polymorphism.

A justification for this prediction protocol lies in whether or not the model is able to pass the so-called *model test* to predict its own data. Here is how the model test is carried out. For a parameter set, say for a brush-legged fixation, we first generate a sequence of the "observed" data N_r, N_ℓ by the model at the corresponding state $x = p = 0$ for a finite number of generations. Call it *simulated model data*. We then fit the model to this data by the line search method. If a majority of the best fits predict a brush-legged fixation, then the model passes the model test at the given parameter. Ideally we want the model to pass the test at every parameter point for each of the three fixation cases. In practice we can only run the test at a few selected parameters, often at random, for each case. If the model passes this random model test, a self-imposed consistency test, then the model is considered to be capable of making predictions of empirical data. This model test protocol by the majority rule can also be extended to one by the best fit rule. (The existence of the absolutely global minimum $E = 0$ is given because the model is best fitted to its own data. But finding it by the random line search is another aspect of the model test to simulate the blind best fit to the empirical data.) The more tests a model is able to pass the better it is, which turns out to the case for both the *a*-recessive and the *a*-dominant models as we will show below.

Best model fit result: Since a field estimate puts the rock substrate proportion between 5% and 15% and because we assume that all female spiders are imprinted to favor brush-legged males, the following constraints

$$\nu_r \geq 1, \ \nu_\ell \geq 1, \quad \text{and} \quad 0.05 < r < 0.15 \tag{10}$$

are included in the line search for best fit of Equations (2) and (7) to the data. Since it is generally expected to have many local minimizers $E(\rho^*)$ and there are no effective ways to know *a priori* where the global minimizer is, a practical approach to take is to randomly generate initial guesses for multiple runs of the line search. For our search we randomly choose the initial from $0 \leq x_o + y_o \leq 1$ with $p_o = x_o + y_o/2$ and r from [0.05, 0.15], both uniformly, and choose all other parameters with the absolute values of a normal distribution of unit mean and unit standard deviation. For each of the models (2) and (7), a total of 2000 runs were carried out. Some of the key statistics are summarized in Table 2. For the *a*-recessive model, 365 best fits are in the parameter constraint (10). 393 is the same number for the *a*-dominant model. (Spurious fits with x_o, p_o not in the range $0 \leq x_o + y_o \leq 1$ with $p_o = x_o + y_o/2$ are automatically rejected.) It shows that a majority of the best model fits are of the polymorphism case, with 77% and 78.4% for the two models. The initial points and parameter values, together with their sensitivities, of the first best model fit are also listed for each model in the table. It shows that both models are equally plausible for the mixed-population data.

We also tested the *a*-recessive and *a*-dominant models against a background control model which assumes that the MOP trait resides on the male's sex chromosome. The same best-fit exercise was carried out. Like the two autosome cases polymorphism was established but the best-fit error was 0.0921 instead, a relative error of 23% over the autosome models even though all models have exactly the same number of parameters.

The result of model test for both models is given by Table 3. The 0-stable parameter (P_o<1) selected for each model's simulated data is the best fit of the model to the mixed-population data that is of the (P_o<1)-case. The 1-stable parameter, and the polymorphism parameter are selected similarly. The simulated model data are four generations in length, the same as for the 05–08 data of the mixed population. The same random 2000 line search initials as for the mixed-population data are used for

Table 2. Best model fit result.

Equilibrium type	*a*-Recessive (365 total)		*a*-Dominant (393 total)	
$P_0>1$, $P_1>1$	281 (77.0%)		308 (78.4%)	
$P_0<1$	28 (7.7%)		81 (20.6%)	
$P_1<1$	56 (15.3%)		4 (1.0%)	
Parameter	**Best fit**	**Sensitivity**	**Best fit**	**Sensitivity**
x_0	0.3528	1.1456	0.0815	0.0649
p_0	0.6222	13.522	0.2145	4.4917
u_r	2.5518	0.6525	2.4971	0.6214
u_l	0.3854	3.3785	0.3753	4.2830
v_r	1.1366	0.0062	1.0494	0.0022
v_l	2.2335	0.7631	2.5130	1.2975
r	0.1337	0.0193	0.0616	0.0044
Error E	0.0746		0.0746	
Protected polymorphism	P_0=1.0525, P_1=1.1335		P_0=1.0185, P_1=1.0465	

Table 3. Model test.

Prediction	Simulated model data type					
	a-Recessive model			*a*-Dominant model		
	$P_0<1$	$P_1<1$	$\{P_0>1, P_1>1\}$	$P_0<1$	$P_1<1$	$\{P_0>1, P_1>1\}$
$P_0<1$ (%)	**68**	0	4	**68**	0	17.4
$P_1<1$ (%)	26	**100**	33	26	**100**	4.4
$P_0>1, P_1>1$ (%)	6	0	**63**	6	0	**79.2**
Total	2000	1848	542	2000	2000	564

the model test. The number in the total row is the number of the best model fits inside the parameter constraint (10). Notice that the percentage (68%) for the 0-stable test of the *a*-recessive (and the *a*-dominant) model is not as high (100%) as for the 1-stable test. This is due to the fact the 0-stable parameter has a rather low $P_1>1$ value, which in turn pulls some best fits (26%) to the ($P_1<1$)-class. For the polymorphism test for the *a* -recessive model it is because the polymorphism equilibrium point is closer to the $x=p=1$ equilibrium than to the $x = p = 0$ equilibrium. In addition, the 33% of the ($P_1<1$)-class has many high fit error E as their best fits to the simulated polymorphism equilibrium move away from it in transience. A few more random simulations demonstrate similar trends: the more distinguished a test parameter is from the case boundaries $P_0=1$, $P_1=1$ or/and a polymorphism equilibrium point is from the trivial equilibria, the higher passing percentage the model scores on the test. No false positive prediction by either model of the majority prediction rule or of the best model fit rule was encountered by sample runs numbered over 1000. It is because of this validation of the model test that the polymorphism prediction of the mixed-population by the two models (Table 2) is made.

Figure 1(b) is a statistical portrait of the best model fit for the *a*-recessive model. It shows that of the 365 best fits the fit error has a very small variance, and that the best fits are overwhelmingly protected polymorphism. Figure 1(c) shows the predicted time series of the survival probability N_1 for the first 50 best model fits. The aggregated fit (solid-bold line) is computed at each generation to be the mean value of the corresponding substrate N_1 values of the best 50 fits at the given generation. The simulation was run for 1000 generations and all aggregated curves reach a respective equilibrium after 200 generations, thus predicting a dimorphic coexistence for the mixed population. Notice that not all best fits converge to the aggregated dimorphic equilibrium, some appear to trend toward the two monomorphic fixations even though their fit errors deviate little from the mean fit error. That is, one cannot automatically conclude just by the appearance of the data that the mixed population is at a dimorphic equilibrium. Figure 1(d) shows the multivariable function E in each variable's section view when all normalized in the percentile change $(\rho_i-\rho^*_i)/\rho^*_i$. In doing so the concavity of the function $E(\rho)$ can be compared amongst all parameters and initial frequencies because the percentile change is scale-free, and the sensitivity is scale-free as well. Each plotted sensitivity curve is aggregated over all best fits (365 for the *a*-recessive model and 393 for the *a*-dominant model). The same aggregation was also investigated for the first 50, 100, 200 best fits, and the best fits which are limited only to polymorphism. With only the exception of the initial value x_0, there is little quantitative change for the aggregated sensitivities. It shows that the best model fit is least sensitive to parameter r and v_r. For example, doubling the v_r parameter value leads to little change in the fit error E for almost all best fits. The same variable best fits were also used for Figure 1(b,c), the respective quantitative conclusions are the same.

Figure 2 shows the bifurcations of dimorphism with changes in the system parameters. Figure 2(a) is a bifurcation plot in u_r vs. r. At the center of the diagram is the best model fit. The region left of the left dash curve represents a numerical fixation by the non-ornamented males and the region right of the right dash curve represents the same by the brush-legged males. The system can theoretically change from the non-ornamented male domination to coexistence (middle region) and to the brush-legged male domination as r changes from 0 to 1 along any fixed $u_r>1$. We note that since parameters u_r and v_r can be combined into one parameter $w_r = u_r v_r$, the bifurcation diagram in v_r vs. r (not shown) is qualitatively the same as Figure 2(a) with the vertical axis scaled by the best value v_r. It is because of this property for the u_r,v_r pair and for the u_ℓ,v_ℓ pair that only two bifurcation diagrams are shown. From Figure 2(b) we can see that a small increase in female's preference to the brush-legged males in the leafy substrate can easily tip the dimorphic coexistence to a fixation by the brush-legged males as the best fit point is near the boundary. It is theoretically possible for the system to change to a fixation by the non-ornamented males if the females become selectively neutral ($v_\ell=1$) in the leafy substrate. Because of a similar reason as before this bifurcation diagram stays the same qualitatively if we substitute u_ℓ for v_ℓ or v_r for u_r.

The same analyses above were carried out for the *a*-dominant model, the corresponding quantitative results remain the same as well.

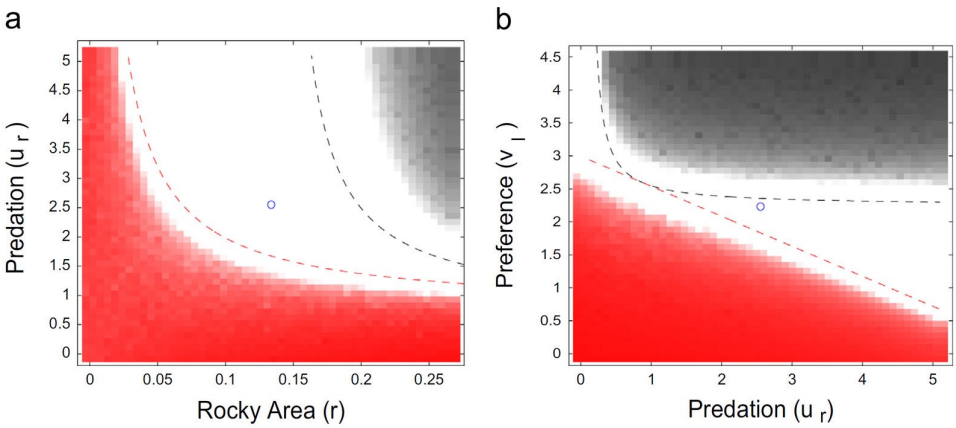

Figure 2. Bifurcation diagrams for the best model fit to the 05–08 data for the *a*-recessive model in the range (10). The dashed curves are the theoretical bifurcation curves, P_o=1, P_1=1. Each diagram was generated on a 50×50 grid with the best-fitted point at the center. The model at each grid point was run for 1000 generations. The shorter generation time the population takes to be within 0.01 of the fixating equilibrium, the darker the shade is for the corresponding parameter point, and the shade level is averaged over 10 arbitrarily chosen initial states. White region represents no entering the 0.01 range of either trivial equilibrium by the 1000th generation. The lower-left region is for the fixation by non-ornamented males, and the upper-right region is for the brush-legged males. The same diagrams for the *a*-dominant model are qualitatively similar.

4. Discussion

The propensity of our best model fit strongly supports the case that the mixed-population system is of Levene's polymorphism type. Further support by empirical studies on system and model parameters are

1. The ornamented male form is naturally selected on rocks (u_r >1), and against in litter (u_ℓ < 1). The latter is qualitatively consistent with the laboratory study of Pruden and Uetz (2004) about the predation effect by the common predator *H. helluo* on the two male forms in equal numbers. Since *H. helluo* is commonly found in leafy substrate, we can use the mean u_ℓ value for best fits (Figure 1(b)) to get a quantitative calibration on the predation ratio $N_1(0.5,u_\ell)/N_2(0.5,u_\ell) = 1/u_\ell = 1/0.3949$–2.5323, consistent with the predation study that *H. helluo* has twice as much predatory response to *S. ocreata* than *S. rovneri* (Pruden and Uetz, 2004, Figure 2). However, the study of Fowler-Finn and Hebets (2011b) showed—with this very population—that the mortality from predation is equal between the two forms from *H. helluo*. These studies together seem to suggest that other predators (the jumping spiders *Phiddipus clarus*, the American toad, *Bufo americanus*, and various bird species) may differentially predate the two forms as well (Pruden and Uetz, 2004; Roberts et al., 2006; Roberts and Uetz, 2008). The study of Lohrey et al. (2009) shows that avian predators may have been a selection factor in shaping the behavior of *S. ocreata*.
2. The laboratory study of Hebets and Vink (2007) shows that the females are 3.0–6.5 times more likely to mate with the brush-legged males than the non-ornamented ones (Figure 4 of Hebets and Vink, 2007). Our best model fit is consistent with this result. In particular, the mean value of v_r is about v_r = 2 (Figure 1(b)) but the insensitivity range is large, about −50 to 250 in percentile around the mean (Figure 1(d)), making the predicted preference range approximately 1–5. The predicted preference range is smaller for the brush-legged male form in the leafy substrate with a mean near 2 and more restricted sensitivity. The latter is consistent with the finding by Scheffer et al. (1996) that vibratory displays by the *S. ocreata* males to attract the attention of the females are less effective in the leafy substrate.
3. All best fits are most sensitive to the brush-legged male's natural selection disadvantage in litter, suggesting that there may be a predator lurking exclusively in the leafy substrate that preys upon the brush-legged males more so in proportion than the non-ornamented males, again consistent with the finding of Pruden and Uetz (2004).

More predictions are listed below, some of which are also qualitatively consistent with what biologists know about the mixed population:

1. All best fits are least sensitive to female's mating preference to the brush-legged males on rocks, implying that the preference can be considerably greater than what the best-fit suggests, and that the rock substrate is the preferred habitat of the brush-legged males.
2. All best fits are sensitive to the brush-legged male's sexual selection in the leafy substrate, implying that the female may apply a greater effort in seeking out the brush-legged males in litter than on rocks due to the former substrate's constraint on brush-legged male's acoustic signaling.
3. All best fits are not sensitive to the spatial heterogeneity in parameter *r*, suggesting that the coexistence of the two male forms can persist against large variations in rocky-leafy proportion (Figure 2(a)). The insensitivity also suggests that the distinction or mix of the two substrate types can be more or less pronounced in composition.
4. The best fit is more sensitive to natural selection (larger $S(u_r),S(u_\ell)$) than to sexual selection (smaller $S(v_r),S(v_\ell)$ in the two substrates). This cannot be explained by the fact that the observable variables $N_1(x_o,u_i)$ depend only on the natural selection parameter u_i since $S(u_r)$ is lower than $S(v_\ell)$. These observations together seem to suggest that the polymorphism of the mixed population has been shaped more by natural selection than by sexual selection.
5. A fixation by the brush-legged male form may happen if it is preyed less in litter than the best fitted intensity (Figure 2(b) with u_ℓ substituting for v_ℓ). This implies that by reducing the predatory pressure, the brush-legged male form may take over the mixed population site. Similarly, the system can go all the way to a non-ornamented fixation by significantly reducing the rock proportion. Both imply that a greater effect natural selection can have on the system.

As for what one can infer about some theoretical issues from the model, our result suggests that the fitness parameters

($\bar{w}_r = \bar{u}_r \bar{v}_r \sim 5$) can be far away from the Hardy–Weinberg neutrality ($u_i = v_i = w_i = 1$), contrary to the expectation that such opposing selection on genotypes should be small (Maynard Smith, 1970; Prout, 2000). Also, because of the relaxed constraint on the spatial heterogeneity (small $S(r)$), Levene's polymorphism mechanism is rather robust. This suggests that the mechanism may not be as rare as suggested by Prout (2000) for the maintenance of polymorphism in nature. Finally, Figure 1(c) suggests that by altering the substrate ratio r, monomorphic fixation can be reached in 20–50 generations, contrary to the long fixation time suggested by Livingstone (1992).

Both models (a-recessive and a-dominant) predict Levene's polymorphism for the mixed population, but the best model fit does not favor one over the other. This seeming limitation is oddly consistent with the limited laboratory study (Stratton and Uetz, 1986) that although the two male traits are autosomal for both *S. ocreata* and *S. rovneri* species, they are not perfectly Mendelian nor with a clear recessive vs. dominant designation. The male dimorphism seems to be not determined by a single locus. Even less is known for the mixed population. This is one aspect in which the model can be further refined. It also represents one area where a more sensitive detection method can be developed to determine which of the two models is closer to the mixed-population system.

Lastly, since polymorphism is thought to be a precursor to sympatric speciation, the way by which the mixed population's male dimorphism is maintained might be how a *Schizocosa* population did before splitting to *S. ocreata* or *S. rovneri* because of opposing predation selection on the two male forms in isolated habitats with varying degrees of spatial heterogeneities, some favored the brush-legged male form and some others favored the non-ornamented one. That is, natural selection might be the key speciation determinant, or the simplest and the easiest route to speciation for both species before reproductive isolation was completed by female's discrimination of the species-specific male courtship.

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Appendix A.

Without niche selection, the conditional zygotic frequencies in each substrate before natural and sexual selections for the male are the same as the non-conditional ones. Then the survival probability distribution becomes $N(x,u_i)aa : (1 - N(x,u_i))[aA + AA]$ where

$$N(x,u_i) = \frac{x}{x + u_i(1-x)}$$

This survival probability is then weighted by female's mate choice ratio $1aa : v_i[aA + AA]$ to derive the male's reproductive distribution $N(N(x,u_i),v_i)aa : (1 - N(N(x,u_i),v_i)))[aA + AA]$ where $N(X,v_i) = X/(X + v_i(1 - x))$ is the re-proportionate quotient by sexual selection on survived male distribution $Xaa : (1 - X)[aA + AA]$. It is straightforward to verify that the composition simplifies to $N(N(x,u_i),v_i) = N(x,u_iv_i)$ and hence the overall substrate-specific fitness parameter $w_i = u_iv_i$.

Appendix B.

We note that Equation (2) is a linear function in r. Hence, its transformed equivalent form Equation (3) must be linear as well. Therefore, to verify the latter we only need to verify it at two r values, $r = 0$ and $r = 1$, at which the habitat is homogeneous. Since all homogeneous cases have the same mathematical form, we only need to verify one case, i.e. $x' = p^2 + p(1 - p)x\phi(x,w,0,1)$, $p' = p + \frac{1}{2}(1 - p)x\phi(x,w,0,1)$ with $\phi(x,w,0,1) = (1 - w)/(w + (1 - w)x)$. To simplify, we let $\psi(\varepsilon x,p) = (1 - p)x\phi(x,w,0,1) = \varepsilon x(1 - p)/(1 + \varepsilon x)$ with $\varepsilon = 1/w - 1$. Then, we only need to show $x' = p^2 + p\psi(\varepsilon x,p)$ and $p' = p + \frac{1}{2}\psi(\varepsilon x,p)$. To this end, we note first that using (1) and (2) with $r = 1$, $w_r = w$, Equation (2) can be rewritten as

$$\begin{cases} x' = p_m p_f = \left(\alpha x + \dfrac{\beta}{2} y\right)\left(x + \dfrac{1}{2} y\right) \\ y' = 1 - p_m p_f - (1 - p_m)(1 - p_f) = 1 - \left(\alpha x + \dfrac{\beta}{2} y\right)\left(x + \dfrac{1}{2} y\right) - \beta\left(1 - x - \dfrac{1}{2} y\right)^2 \\ \alpha(x,w) = \dfrac{1}{w + (1-w)x}, \quad \beta(x,w) = \dfrac{w}{w + (1-w)x} \end{cases}$$

with $p_m = p_{m,i}$, etc. by dropping off $i = r,\ell$. Next we replace y by $y = 2(p - x)$ throughout Equation (11). Verify next that $x' = (1/(1 + \varepsilon x))(\varepsilon x + p)p$ from the first equation of (11) and $p' = x' + y'/2 = (\frac{1}{2}(1 + \varepsilon x))(\varepsilon x(1 + p) + 2p)$ from the first and the second equations of (11). Then verify that $(x' - p^2)/p = \psi(\varepsilon x,p)$ and $2(p' - p) = \psi(\varepsilon x,p)$ to complete the verification. Note that the original domain $\{0 \le x + y \le 1\}$ is transformed by the change of variables $x = x$, $p = x + \frac{1}{2}y$ into $p \ge x$ but $p \le x + \frac{1}{2}(1-x) = (x + 1)/2$.

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